

RESEARCH ARTICLE

Dragonflies use underdamped pursuit to chase conspecifics

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ABSTRACT

Pursuit is a common behavior exhibited by animals chasing prey, competitors and potential mates. Because of their speed and maneuverability, dragonflies are frequently studied as a model system for biological pursuit. Most quantitative studies have focused on prey pursuits in captive environments. To determine whether a different pursuit strategy is used when chasing conspecifics of nearly equal speed and agility, we recorded 3D flight trajectories from nine territorial chases between male *Erythemis simplicicollis* dragonflies in natural field conditions. During chases, dragonflies used an interception strategy with an unusually high-magnitude gain ($k = -10.03 \text{ s}^{-1}$ horizontal; -8.86 s^{-1} vertical) and short time delay ($\tau = 50 \text{ ms}$). The product $k\tau$ determines how aggressively a pursuer corrects course to achieve interception. Previous studies of prey pursuit have found $k\tau$ values close to $-1/e$ (-0.37), the time-optimal value for achieving pursuit without overshooting. However, we found that dragonflies chasing conspecifics use more negative $k\tau$ (-0.50 horizontal; -0.44 vertical), resulting in pursuits with a high degree of overshooting (i.e. moving past the target and alternating position from side to side). We confirmed via simulation that the observed gain and delay produce overshooting. We propose that overshooting is an adaptive feature of conspecific chases that can be achieved with only slight modification of the strategy used for intercepting prey. Overshooting might help avoid potentially damaging collisions while exhibiting the pursuing animal's flight performance and competitive ability. Repeated close approaches might also evoke evasive responses from the other dragonfly, effectively herding the competitor out of the territory.

KEY WORDS: Interception, Territoriality, Guidance, Control, Kinematics, Videography

INTRODUCTION

Many animals engage in pursuit behaviors, maneuvering in air, water or on land to chase prey, competitors or potential mates. Pursuit requires an organism to respond to rapidly changing sensory cues, often while exhibiting high locomotor performance (Aoki et al., 2012; Bomphrey et al., 2016; Wilson et al., 2018). The pursuit strategy an animal uses to control its path relative to the target's motion and to make adjustments as the target changes speed or direction has implications for the efficiency and success of the pursuer (Pal, 2015). Studies on insects, birds and mammals have elucidated simple control models that allow pursuers to efficiently

catch targets (Brighton et al., 2017; Collett and Land, 1978; Ghose et al., 2006; Olberg et al., 2007).

Several pursuit strategies have been described in the literature (Pal, 2015). Perhaps the simplest is tracking (also known as direct pursuit or classical pursuit), in which the pursuer maneuvers toward the current position of the target (i.e. the direction of the range vector). This produces a curved path as the pursuer shifts direction to aim at the moving target's changing position. Tracking has been documented in conspecific chases in houseflies (Land and Collett, 1974), pursuit of falling food by teleost fish (Lanchester and Mark, 1975) and prey pursuit in tiger beetles (Gilbert, 1997).

An alternative to tracking is interception, in which the pursuer aims for a point ahead of the target to minimize time to capture. Interception can be achieved through a constant bearing (CB) geometry, in which the bearing angle ϕ [i.e. the angle separating the range vector (\mathbf{r}) and the pursuer flight vector (\mathbf{P}); see Fig. 1] is held constant. This strategy is used, for example, by people catching baseballs (McBeath et al., 1995) and dogs catching frisbees (Shaffer et al., 2004). Another geometry that achieves interception is constant absolute target direction (CATD), where the absolute target direction α is held constant (Ghose et al., 2006). Evidence supporting CATD has been found in bats (Ghose et al., 2006), dragonflies (Olberg et al., 2000), hawks (Kane et al., 2015) and falcons in the final stages of target interception (Brighton et al., 2017). It should be noted that the terms CATD and CB have been used variably in the literature, but here we use the definitions given by Ghose and colleagues (2006).

We examine basic implementations of tracking and time-optimal interception (see Materials and Methods), in which the pursuer turns such that the rate of change of the error angle (the angle between the 'desired' flight direction and the actual flight direction) is directly proportional to the magnitude of the error angle. These models have been found to describe pursuit in many of the species mentioned above, including beetles, flies, water fleas, dragonflies and bats. We also examine a guidance law called proportional navigation (pro-nav), in which the pursuer adjusts its steering with a variable gain to counter changes in the relative direction of the target (Shneydor, 1998). Depending on the specific gain, pro-nav can produce a variety of pursuit geometries, including tracking and interception trajectories and is used by falcons during prey pursuit (Brighton et al., 2017).

Some animals switch pursuit strategies in different conditions. Hoverflies use both tracking and interception to pursue conspecifics (Collett and Land, 1975, 1978), and goshawks use tracking to approach stationary prey and lures, but CATD interception to chase moving prey (Kane et al., 2015). Little is known, however, about how or when a species adapts or switches its pursuit strategy to handle different situations.

Dragonflies have been studied as a model for pursuit because they use fast, agile flight for a range of behaviors (Bomphrey et al., 2016). Olberg and colleagues found that in large naturalistic enclosures, *Erythemis simplicicollis* dragonflies use interception to capture both natural and artificial prey (Olberg et al., 2000, 2007).

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List of symbols and abbreviations

CATD	constant absolute target direction
CB	constant bearing
E	evader's flight vector
IMU	inertial measurement unit
k	gain
P	pursuer's flight vector
P_o	optimal interception vector
r	angle from pursuer to evader (range vector)
R	reference vector
U_E	evader's speed
U_P	pursuer's speed
α	angle between reference vector and range vector
β	angle between range vector and evader's flight vector
γ	quintic spline function
τ	reaction delay
θ	angle between pursuer's flight direction and a reference vector
ρ	turn radius
ϕ	bearing angle
ϕ_e	difference between optimal bearing angle and actual bearing angle (error angle)
ϕ_o	optimal bearing angle for interception

Mischiati and colleagues expanded on this finding, reporting that *Plathemis lydia* dragonflies use internal models of their own movements and that of prey to maneuver into a favorable orientation for prey capture before using interception for the final stage of the pursuit (Mischiati et al., 2015). Male dragonflies of multiple species also engage in territorial pursuit, flying at and chasing rival males who enter their territory (Bomphrey et al., 2016; Schultz and Switzer, 2001). Mizutani and colleagues proposed that territorial *Hemianax papuensis* dragonflies use a type of pursuit known as motion camouflage, in which the pursuer moves to hold a constant

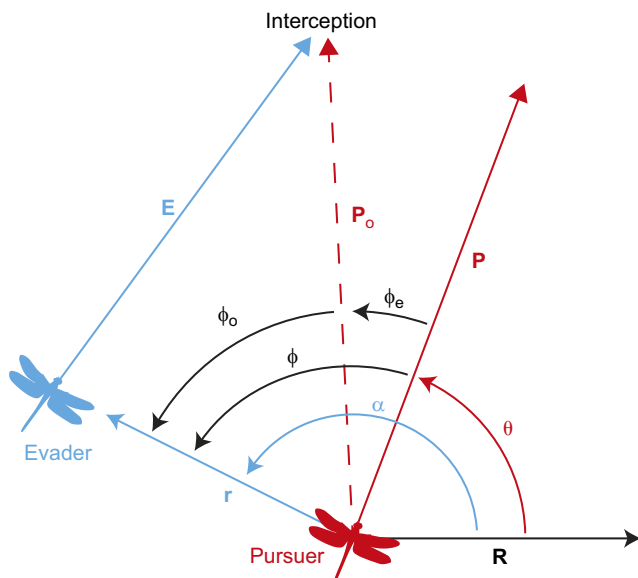


Fig. 1. Angles of interest during pursuit. The pursuer's flight direction (P) is measured as the angle θ relative to the reference vector R . The range vector (r) is the vector between the pursuer (P) and evader (E). The absolute target direction α is the angle between the reference vector and range vector. The bearing angle ϕ is the angle separating P and r . The optimal interception vector (P_o) is the flight vector that, at the pursuer's given flight speed, will result in fastest interception. The optimal bearing angle ϕ_o is the angle separating P_o and r . The angle ϕ_e gives the difference between the observed bearing angle ϕ and the optimal bearing angle ϕ_o .

position on the evader's retina, thus disguising itself as an inanimate object; however, evidence for this result is limited to short sections of pursuit (Mizutani et al., 2003). While the mechanics and strategies of dragonfly prey pursuit have been studied in some depth (Combes et al., 2012; Mischiati et al., 2015; Olberg et al., 2000, 2007), territorial chases are still largely uninvestigated (Bomphrey et al., 2016). Furthermore, few studies of dragonflies have been conducted in the field, and the range of flight performances exhibited by dragonflies under natural conditions is unknown.

Here, we report on territorial chases between male *E. simplicicollis* dragonflies interacting under natural field conditions. We applied a variant of a recently developed field-recording technique, rotational stereo videography (de Margerie et al., 2015), to overcome the limitations of fixed-camera videography. We quantify the conspecific-chase pursuit strategy, reaction latency and flight trajectory kinematics, and compare these results to pursuit simulations and to prior research on prey pursuit. We demonstrate that dragonflies use an aggressive interception strategy that causes overshooting of the target. We argue that this behavior is adaptive for a pursuit scenario where the goal is to drive away the target rather than intercept it.

MATERIALS AND METHODS**Data collection**

We filmed male eastern pondhawk dragonflies *Erythemis simplicicollis* (Say 1839) performing conspecific territorial pursuits along the shore of Lake Ellen in Chapel Hill, NC, USA (35.946°N, 79.053°W) across 8 days on 20–28 August 2016. We recorded along approximately 50 m of open, grassy lakeshore. In preparation for recording, we stationed the recording apparatus (described below) by the shore near an area where we could see multiple *E. simplicicollis* dragonflies. In a total 4.7 h of video, we found nine *E. simplicicollis* conspecific pursuits in which both dragonflies were clearly visible throughout the interaction. All observed chases occurred under sunny conditions with little to no wind. We noted species as determined using visual identification cues at the time of recording. We confirmed that all recordings were between male *E. simplicicollis* based on sexually dimorphic visual markings. We were unable to identify individuals in the field; therefore, it is possible that we recorded a single individual in multiple interactions. However, we took efforts to avoid this scenario, including frequently changing the section of the lakeshore being recorded, and recording at locations where numerous individuals were present (up to six male *E. simplicicollis* dragonflies were observed simultaneously). Multiple dragonflies were often active in brief flurries; one such event included, in an 8 s span, three chases involving at least four separate individuals. No other digitized chases were clearly connected in space and time.

Stereo rotational videography and data processing

To film chases, we used a modified version of stereo rotational videography (de Margerie et al., 2015). Our apparatus allowed us to pan and tilt to follow the path of the dragonfly, or simply change the filming location (and dragonfly territory) without camera recalibration. Our apparatus used two GoPro Hero3 Black cameras operating in 1080p Narrow view mode at a 59.94 fps record rate, one mounted on either end of a 65-cm-long aluminum rod. We attached the center of the rod to a tripod with a rotatable pistol ball grip head, and we mounted an inertial measurement unit (IMU) (SUNKEE 1232055 10DOF 9-Axis Attitude Indicator, Sunkee, Amazon, Inc., Seattle, WA) at the center of the rod. We then used previously established methods (Jackson et al., 2016; Theriault

et al., 2014) to calibrate the cameras, digitize the chases, and extract 3D paths of the dragonflies in the local reference frame of the rotating cameras. We smoothed the resulting dragonfly trajectories to the 95% confidence interval of the underlying $[x, y, z]$ coordinate measurements, with an additional 1.2 pixels of digitizing uncertainty added. The additional uncertainty was required to make the same dragonfly trajectory produce >95% similar accelerations when digitized by different researchers.

In chases (four out of ten) in which the cameras were rotated during filming, we next digitized two stationary points (such as rocks), which were used along with the fact that the camera pivot remained in place to create a single stationary reference frame onto which we transformed the dragonfly tracks. Before transformation, we smoothed the stationary point time series using the same procedure described above for the dragonflies. With a sensor fusion algorithm based on a Kalman filter, we then used the IMU readings to determine the orientation of the camera rig in the stationary reference frame relative to our global gravity vector calculated during initial calibration (Leccadito, 2013). We transformed all points from the stationary reference frame into a global, gravity-aligned reference frame. For quality assurance, we digitized additional stationary points for the durations of two chases and applied the transformation to these points; a successful transformation would result in these points appearing not to move. The mean error in stationary point position (that is, the average distance between all post-transformation positions and mean post-transformation position) was 19.7 ± 15.4 mm (mean \pm s.d.). In chases (six out of ten) in which no camera motion was needed to follow the dragonflies during the pursuit, we used the IMU data to transform the tracks into a gravity-aligned reference frame.

Identifying pursuers and evaders

We used time-delayed correlations in turn rate to identify pursuers and evaders and to isolate sections of videos that were included in our analysis. To calculate the time-delayed turn correlation, we windowed turn rates of both dragonflies using a window size of 500 ms. For each time point in the sequence, we determined the time delay within the range of ± 200 ms that yielded the highest correlation coefficient; we classified the dragonfly that acted first as the evader. For analysis, we identified sections of interactions with consistently high time-delayed turn rate correlations (>0.75). This procedure was inspired by the time-delayed directional correlations and time-delayed spatial correlations proposed previously for identifying pursuits (Giuggioli et al., 2015). However, the metrics proposed previously are better suited for pursuits involving tracking than pursuits using interception. Here, we found that turn rates were more robust measures for determining actor and reactor.

After identifying the pursuer and evader, we calculated several pursuit angles for each frame (Fig. 1). These angles are calculated separately in the horizontal and vertical planes. The bearing angle ϕ is taken as the 2D angle separating the pursuer's flight vector (\mathbf{P} in Fig. 1) from the range vector (\mathbf{r}). The optimal flight angle for achieving interception (ϕ_o) was calculated from the pursuer's speed (U_P), the evader's speed (U_E) and the angle β separating the range vector and the evader vector (\mathbf{E}):

$$\phi_o = \sin^{-1} \frac{U_E \sin \beta}{U_P}. \quad (1)$$

The angle ϕ_e is taken as the difference between the bearing angle ϕ and the optimal bearing angle ϕ_o (Fig. 1).

Pursuit strategy analytical framework

We first tested a feedback implementation of tracking and a similar implementation of time-optimal interception. In tracking, the pursuer brings ϕ to zero, and under this model, the pursuit is described by a time-delayed differential equation (Bellman and Cooke, 1963):

$$\frac{d\phi(t)}{dt} = k\phi(t - \tau), \quad (2)$$

where k is a negative gain parameter and τ is the reaction. Alternatively, for interception, the pursuer brings ϕ_e (see Fig. 1) to zero:

$$\frac{d\phi_e(t)}{dt} = k\phi_e(t - \tau). \quad (3)$$

After finding support for this interception model (see Results), we tested whether a CB or CATD geometry described the pursuit. As noted by Ghose et al. (2006), the geometry of the pursuit (Fig. 1) shows us that $\alpha = \theta + \phi$ and therefore:

$$\frac{d\alpha}{dt} = \frac{d\theta}{dt} + \frac{d\phi}{dt}. \quad (4)$$

In CB, the pursuer maneuvers to keep ϕ at a constant value, and therefore:

$$\frac{d\theta(t)}{dt} = \frac{d\alpha(t - \tau)}{dt}. \quad (5)$$

Alternatively, in CATD, the pursuer maneuvers to keep α at a constant value, and therefore:

$$\frac{d\theta(t)}{dt} = -\frac{d\phi(t - \tau)}{dt}. \quad (6)$$

We also tested for proportional navigation pursuit, which can be considered a more general case of CB pursuit where a gain parameter N is added (Brighton et al., 2017; Shneydor, 1998):

$$\frac{d\theta(t)}{dt} = N \frac{d\alpha(t - \tau)}{dt}. \quad (7)$$

Similarly, we considered a general case of the CATD formulation with an added gain parameter:

$$\frac{d\theta(t)}{dt} = -N \frac{d\phi(t - \tau)}{dt}. \quad (8)$$

To distinguish between different pursuit models, we extracted the time point of each pursuer turn, as indicated by local maxima in the absolute value of pursuer turn rate. For the interaction involving multiple reversals (see Results) between pursuer and evader, we only included the beginning portion of the pursuit sequence until the first reversal. We used linear regression to determine the maximum correlation for the relationships shown in Eqns 2,3 and Eqns 7,8, allowing biologically plausible time delays of up to 200 ms (12 camera frames). Tracking and interception would be supported by high correlations from the relationships shown in Eqns 2 and 3, respectively. Constant bearing and CATD would be supported by high correlations in the relationships shown in Eqns 7 and 8, respectively, and with gains N of approximately 1. Proportional navigation and generalized CATD would be supported by high correlations in Eqns 7 and 8, respectively, with gain N not similar to 1. Because some angles are only defined in two dimensions, we did this analysis separately for the horizontal and vertical planes.

Flight kinematics

For each dragonfly in each chase, we fit a quintic spline function to the smoothed 3D coordinates. The magnitude of the first and second derivatives of these functions (γ' and γ'' , respectively) were taken as instantaneous velocities and accelerations. The turn radius ρ was calculated as:

$$\rho = \frac{|\gamma'|^3}{\sqrt{|\gamma'|^2|\gamma''|^2 - (\gamma'\gamma'')^2}}. \quad (9)$$

Instantaneous velocities and turn radii were used to calculate turn rates and radial accelerations. For each pursuit and evasion sequence, we calculated median and peak kinematic parameters (speed, linear acceleration, turn radius, turn rate and centripetal force). To calculate medians, speeds were sampled once per video frame (60 Hz); all other parameters were sampled at local maxima (accelerations and turn rates) or minima (turn radius).

We conducted pursuit simulations to determine the accuracy with which different pursuit strategies recreated observed pursuit behavior. Simulations were initiated with the observed flight trajectory of the evader and the initial position and flight direction of the pursuer. The observed time delay of 50 ms (three frames) was used in all simulations. The simulated pursuer flight speed was fixed at the observed speed unless otherwise noted. Pursuits were then simulated according to time-optimal interception, proportional navigation, and generalized CATD. We used the method described by Brighton and colleagues (Brighton et al., 2017) for implementing proportional navigation and generalized CATD, using the evader kinematics, pursuer initial position and recorded pursuer speed to simulate the pursuer. For a comparable implementation of time-optimal interception, we adapted this framework and calculated the linear acceleration from the angular acceleration given by Eqn 3.

RESULTS

We quantified nine conspecific pursuits between male *E. simplicicollis* dragonflies lasting 0.48–5.11 s (Fig. S1). In three interactions, a male flew up from a perch in the grass to pursue a dragonfly flying nearby. Five interactions were between two dragonflies that were both flying at the beginning of the interaction. Finally, one interaction was between two males that both flew up from perches in the grass. This was the longest interaction (5.11 s), lasting nearly four times as long as the mean duration of the other 8 events (1.34 s). This interaction between two territorial individuals involved several reversals between which dragonfly was the pursuer and which was the evader, as indicated by the time delay of the maximum turn rate correlation (see Materials and Methods). No such reversals were apparent in the other interactions.

Dragonflies exhibited a wide range of flight performances. Median speeds, turn rates, accelerations and turn radii covered a

345–903% range across interactions (Table 1). The maximum observed speed during any interaction was 8.75 m s^{-1} , and the maximum observed centripetal acceleration was 40.28 m s^{-2} .

Pursuer turn rate followed that of the evader with a short time delay (see example in Fig. 2). The time-delayed correlation coefficient of the pursuer's turn rate and the evader's turn rate (0.5 s windows) exceeded 0.75 during 77% of time points during identified pursuits. The modal time delay for this analysis was 3 frames, or 50 ms.

Median pursuer speed was highly correlated with median evader speed across the 9 interactions (linear regression; $R^2=0.957$; $F=154.8$; $P<0.0001$). The pursuer–evader speed ratio (average pursuer speed divided by average evader speed) ranged from 1.00 to 1.30, showing that pursuers used speeds equal to or slightly higher than evaders. Pursuer flight paths often involved multiple overshoots, with the pursuer's flight path oscillating from side to side over the evader's flight path (Fig. 2).

Pursuit strategy

We found strong support for a time-optimal interception strategy. This is observed in chases as ϕ following ϕ_0 with a short time delay, and ϕ_c approaching zero for much of the pursuit (Fig. 2B). As predicted for interception, Eqn 3 explains a large amount of the experimental data (Fig. 3A), and considerably more so than the predicted relationship for tracking as shown in Eqn 2 (Table 2).

The maximum correlation between $d\phi_c/dt$ and ϕ_c occurred at a time delay of $\tau=50 \text{ ms}$, and gain k of -10.03 s^{-1} in the horizontal plane ($R^2=0.82$; Table 2) and k of -8.86 s^{-1} in the vertical plane ($R^2=0.77$). To determine whether the horizontal and vertical gains were significantly different, we combined the data from both planes and ran a regression test while including an interaction term between the plane and $d\phi_c/dt$. This interaction term was not significant ($t=0.325$, $P=0.74$), indicating that gains do not differ significantly between planes. The parameters we found give $k\tau$ of -0.50 (horizontal) and -0.44 (vertical), which are more negative than the expected optimal value of $-1/e$ (-0.37). These $k\tau$ values would cause the pursuer to exhibit damped oscillations (particularly in the horizontal plane), consistent with observations of pursuer flight paths (Fig. 2).

We found partial support for a proportional navigation strategy in the vertical plane ($R^2=0.61$; Table 2); however, this relationship explained less variation in turn rate than the interception model. In the horizontal plane, the predictions of proportional navigation and generalized CATD explained only a small proportion of data ($R^2<0.1$; Table 2). Gain values (N) from the proportional navigation and generalized CATD models ranged from -0.25 to 0.35 , which was not in alignment with the predictions of CB and pure CATD that $N=1$.

Simulations

We simulated all nine pursuits according to time-optimal interception, proportional navigation and generalized CATD frameworks. Mean errors between simulated pursuit and actual

Table 1. Kinematic parameters of dragonfly conspecific pursuits

	N	Speed (m s^{-1})	Linear acceleration (m s^{-2})	Centripetal acceleration (m s^{-2})	Turn rate (deg s^{-1})	Turn radius (m)
Median	18	3.69 (1.64–5.66)	5.00 (0.10–12.94)	9.51 (2.75–26.66)	145 (47.1–324)	1.80 (0.60–5.42)
Peak	18	4.43 (1.98–8.75)	9.70 (0.49–30.58)	15.48 (2.74–40.28)	276 (47.1–1330)	0.45 (0.003–4.82)

Data are shown as median and ranges (in parentheses) of median and peak values (maxima for speeds, accelerations and turn rates, minima for turn radii) observed in conspecific chases. Because pursuers and evaders had similar kinematic values (see text) data are summarized across both individuals from the nine pursuits.

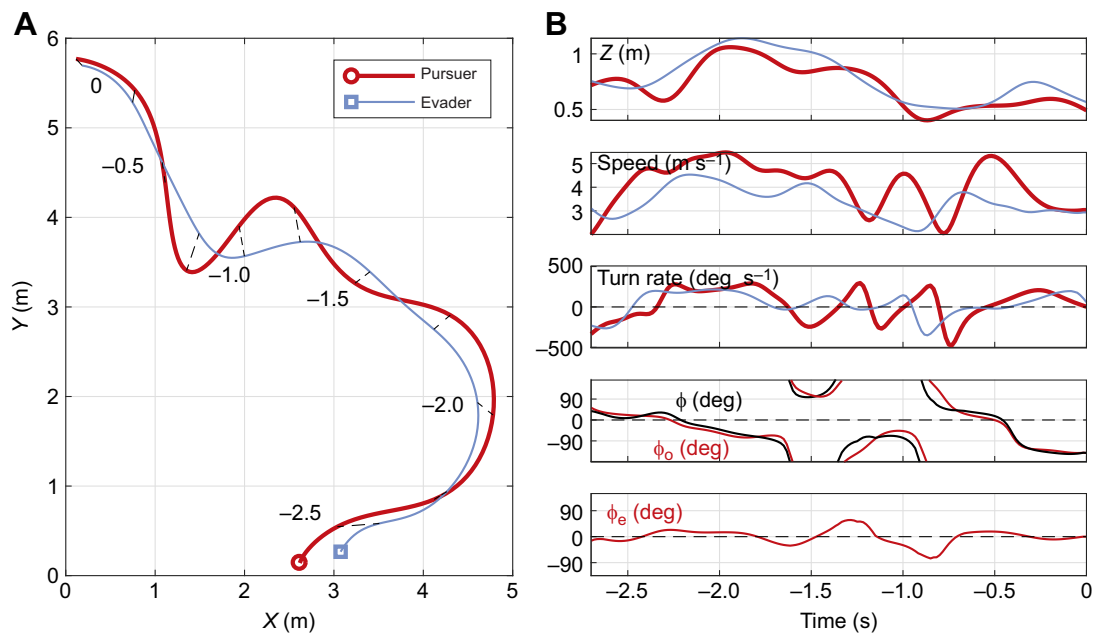


Fig. 2. Example dragonfly pursuit sequence. (A) Overhead view of pursuit. Numbers beside flight paths indicate time until end of trial and dashed black lines indicate relative pursuer and evader positions at 0.25 s intervals. (B) Selected kinematic and pursuit parameters, including Z position (height), speed, turn rate and the pursuit parameters ϕ , ϕ_o and ϕ_e . See Fig. 1 for angle definitions. Note that in A, the pursuer's flight oscillates from side to side over the evader's flight path; in B, the pursuer's turn rate matches the evader's turn rate with a short delay, and ϕ follows ϕ_o , causing ϕ_e to approach zero.

pursuit positions were lowest for the interception model (mean error=0.10 m compared with 0.17 m for proportional navigation and 0.17 m for generalized CATD; Fig. S1). The Nelder–Mead simplex algorithm found that a gain k of -11.30 s^{-1} best recreated observed pursuit trajectories in the horizontal plane for direct interception pursuit (optimization found values of $N=3.3$ for proportional navigation and $N=7.3$ for generalized CATD). The optimized value of k was close to the calculated interception gain of -10.03 s^{-1} (Table 2). The $k\tau$ for the optimized simulation was -0.565 , which is also less than the predicted value of -0.37 . These results provide further support to the hypothesis that dragonflies use time-optimal interception to chase conspecifics.

We conducted additional simulations to examine how gain and speed affect pursuit behavior (Fig. 4). We ran simulations with two speeds – actual speed and reduced speed, where the pursuer averages 130% and 105% of the evader speed, respectively – with the globally optimized gain and higher- and lower-magnitude gains (-7 , -11.3 and -15), and with the observed time delay of 50 ms. The three gain values correspond to $k\tau$ values of -0.35 , -0.565 and -0.75 . Not surprisingly, simulated pursuit with actual speed and the globally optimized gain had the lowest error between simulated and actual pursuit. Higher speeds and more negative gains generated pursuits that were more tortuous and had more overshooting.

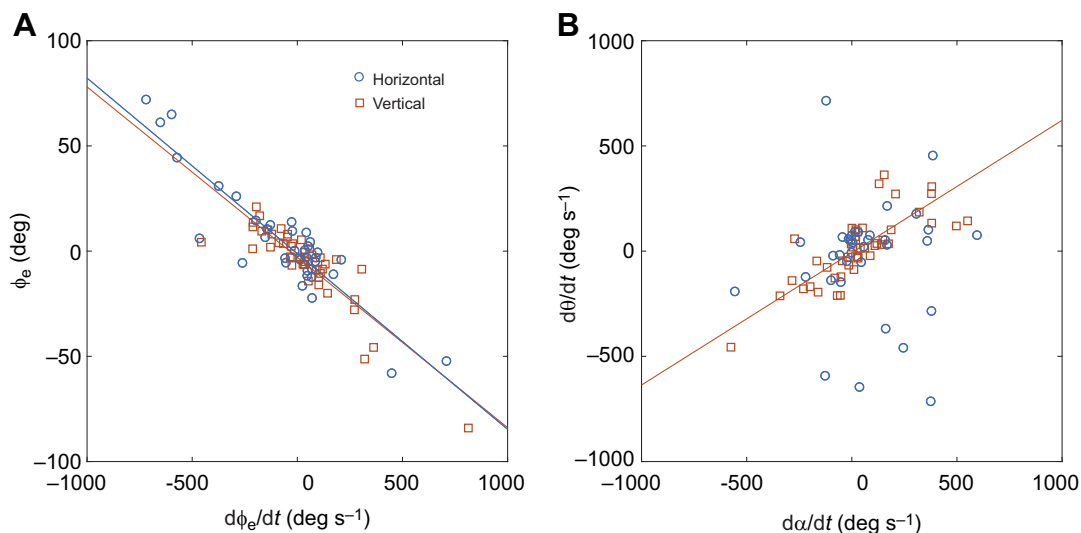


Fig. 3. Analysis of relationships for time-optimal interception and proportional navigation pursuit. (A) High correlations demonstrate strong support for an interception strategy. (B) Partial support for proportional navigation was found in the vertical, but not horizontal plane. See Fig. 1 for angle definitions and Table 2 for statistics. Data points are the local maxima for turn rate in each turn sequence, adjusted for the 50 ms (3 frame) response latency of the pursuer.

Table 2. Statistical analysis of hypothesized pursuit strategies

Pursuit strategy	Plane	Gain k or N	R^2	F	P
Tracking	Horizontal	-11.14	0.54	40.9	<0.0001
	Vertical	0.89	0.01	0.22	0.64
Time-optimal interception	Horizontal	-10.03	0.82	161.7	<0.0001
	Vertical	-8.86	0.77	152.52	<0.0001
Proportional navigation/ constant bearing	Horizontal	0.17	0.02	0.73	0.39
	Vertical	0.58	0.60	64.8	<0.0001
CATD/generalized CATD	Horizontal	0.23	0.10	4.28	0.045
	Vertical	-0.25	0.08	4.05	0.051

See text and Eqns 2–8 for descriptions of analyses. All tests use a time delay of 50 ms. Sample size is 39 turns (horizontal plane) and 51 turns (vertical plane) from nine pursuits (see Materials and Methods).

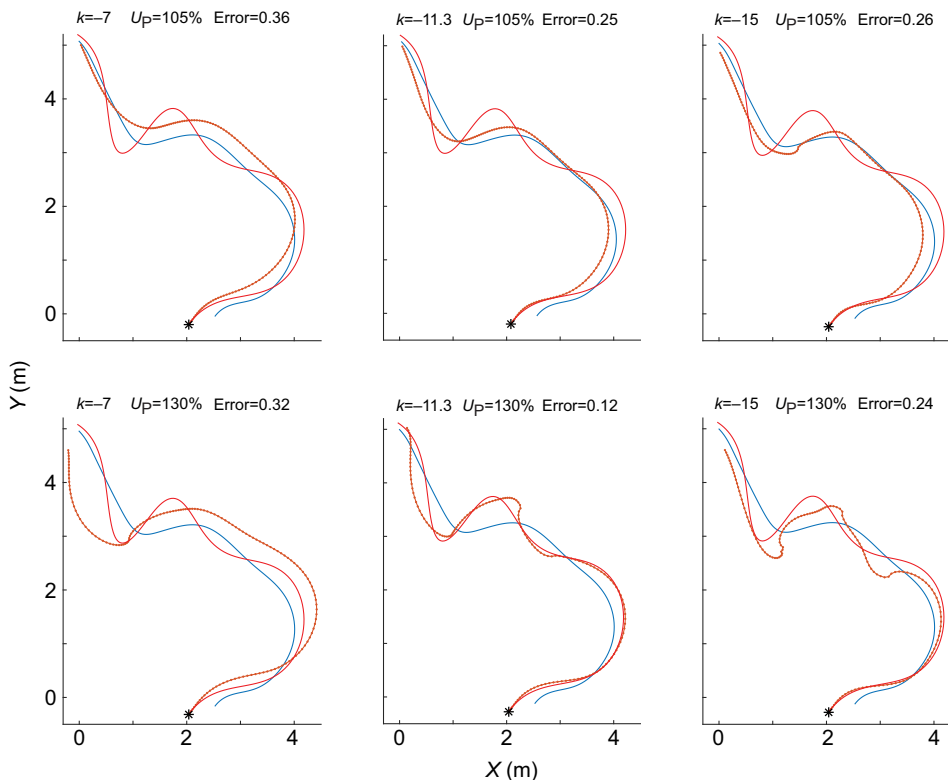
DISCUSSION

We found strong evidence that *E. simplicicollis* dragonflies use time-optimal interception during conspecific territorial chases. Interception can be achieved either through CB or CATD geometries (Ghose et al., 2006; McBeath et al., 1995; Shaffer et al., 2004); however, we did not find support for either CB or CATD pursuit (Table 2), or other control laws including proportional navigation and generalized CATD. These results suggest that, rather than using a heuristic such as CB or CATD, dragonflies directly implement an interception strategy using an internal model of their own motion and that of the evader. We are unable to test this hypothesis more directly with our field data; however, recent research demonstrates that dragonflies are capable of using internal models of their own motion and that of other animals in their environment (Mischiati et al., 2015) and thus might also be capable of the directly implementing time-optimal

interception as described by Eqn 3. Additionally, Collett and Land (1978) propose a method by which hoverflies engaged in conspecific pursuit may be able to calculate an interception course by combining the observed information of the evader's relative angular position and velocity with assumptions about the size and speed of a conspecific and the pursuer's own acceleration. It is possible that dragonflies use a similar mechanism to determine interception angle in conspecific pursuits. Alternatively, dragonflies could be using other mechanisms for implementing interception, such as switching between CB and CATD.

Pursuing dragonflies frequently overshoot their targets, that is, the pursuer crossed over the evader's path multiple times, switching from side to side (Fig. 2). This is partly a result of the high gains used by dragonflies during pursuit. The value of $k\tau$ (see Eqns 2 and 3) determines how rapidly a pursuer corrects its course to achieve interception (or to fly in the direction of the target for tracking). The theoretical optimal value of $k\tau = -1/e$ (-0.37) causes an exponential decay of ϕ (tracking) or ϕ_e (interception) to zero without overshooting of non-evasive targets (dotted gray line in Fig. 5; Erneux, 2009; Land and Collett, 1974). Less negative values of $k\tau$ cause a more gradual decay of ϕ or ϕ_e , whereas decreasing $k\tau$ below $-1/e$ (down to $-\pi/2$) results in underdamped behavior marked by diminishing oscillations (Erneux, 2009). Under these conditions, ϕ or ϕ_e will overshoot (i.e. the dragonfly will over-rotate) while converging to zero. The $k\tau$ values derived from analysis of dragonfly turning behavior (-0.50 horizontal and -0.44 vertical), and from our simulations (-0.565 horizontal) fall within this region, causing ϕ_e to overshoot by 4.0–8.7% of its initial value in the horizontal plane, where most maneuvering occurs. These theoretical results are for a simple evader flying in a straight line; any maneuvers by the evader change the optimal pursuit direction, potentially producing increased oscillations.

Pursuit simulations confirm that the observed pursuit strategy can produce results that are qualitatively and quantitatively similar to the

**Fig. 4. Simulations of dragonfly pursuit.**

Simulations were conducted to model the pursuit sequence shown in Fig. 2 using different gains and pursuer speeds. The pursuer was programmed to follow the evader using only the evader flight path and the actual pursuer's starting position and flight direction. A reaction latency of 50 ms (the delay calculated for the whole dataset) was used for the simulation. The observed pursuer's average speed was 130% of the evader's average speed in this interaction; models were run with actual pursuer speed and reduced pursuer speed (105%) and with gains k of -7 , -11.3 and -15 . As predicted, as the gain and speed increase, the pursuer's path oscillates more and crosses the evader's path more frequently. Values shown above each simulation are the gain k , pursuer speed U_P , and the mean positional error in meters between the simulated and actual pursuer positions across each pursuit sequence.

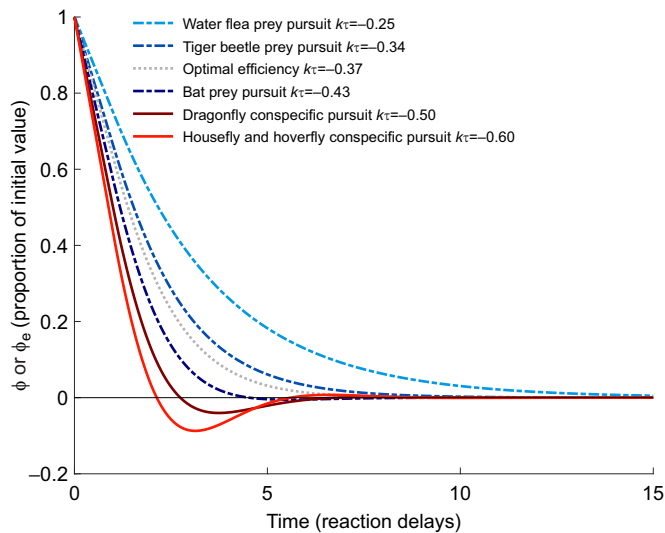


Fig. 5. Comparison of $k\tau$ values across studies, demonstrating how ϕ and ϕ_e change over time (in units of reaction delays). The values shown for dragonfly pursuits were calculated using Eqn 2; values for other species are those and the reported $k\tau$ values in the literature. To achieve the correct heading, a pursuer turns so as to bring ϕ (tracking) or ϕ_e (interception) to 0. The value of $k\tau$ determines how efficiently the pursuer achieves this, and whether the pursuer overshoots the correct angle (in other words, turns too far and has to then turn in the opposite direction). The optimally efficient $k\tau$ value is $-1/e$ (-0.37); at less negative values, the pursuer will take longer than necessary to achieve the correct heading (e.g. water flea prey pursuit), while at more negative values, the pursuer will turn past the correct heading and have to then reverse turn direction (e.g. housefly and hoverfly conspecific pursuit). Note that studies of prey pursuit have $k\tau$ values near, or in one case above the theoretical optimum for minimizing ϕ or ϕ_e without overshooting (i.e. critical damping). In contrast, the three studies on conspecific chases have $k\tau$ with notable overshooting (4.0% in dragonflies and 11.6% in houseflies and hoverflies), a phenomenon known as underdamping.

actual pursuits (Fig. 4). Two important aspects of the dragonfly conspecific pursuit strategy are the $k\tau$ value, and the pursuer's speed relative to the evader's speed. As expected, a more negative $k\tau$ caused more overshooting. Higher speeds also cause more frequent overshooting events because the pursuer closes the distance to the evader more rapidly. Therefore, a dragonfly could reduce the frequency of overshooting by decreasing either the magnitude of $k\tau$ or its relative flight speed.

We currently do not have sufficient comparative data to know whether animals can adjust $k\tau$, or whether it is fixed in the nervous system. This is an interesting question for future studies. However, even if $k\tau$ is fixed, the dragonfly could reduce the frequency of overshooting simply by slowing down. This suggests that overshooting may be an adaptive feature of dragonfly pursuit of conspecifics. Alternatively, high-magnitude gains that produce oscillations during pursuit may be more effective at maintaining close pursuit during territorial chases compared to using critically damped $k\tau$ of $-1/e$. This is because higher-magnitude gains produce faster responses by the pursuer when challenged by a target maneuver. It is notable that the only other studies to quantify $k\tau$ during conspecific pursuit also found underdamped values (Land and Collett, 1974; Collett and Land, 1975).

A comparison of $k\tau$ values across studies and contexts (Fig. 5; Collett and Land, 1975; Ghose et al., 2006; Haselsteiner et al., 2014; Land, 1992; Land and Collett, 1974; Young and Taylor, 1988) indicates that overshooting may be more common in conspecific pursuits, whereas prey pursuits tend to have values closer to the

predicted optimum of $-1/e$. We propose that overshooting is beneficial during conspecific chases. Unlike prey pursuit, the goal of a territorial chase is not to make contact with the target. Colliding with the evader should be avoided as it could be harmful to the pursuing animal. Overshooting is a simple mechanism for avoiding these potentially harmful collisions.

Furthermore, the goal of territorial pursuit flights is to forcefully drive away the competitor or to demonstrate to the competitor that the pursuing animal has superior competitive abilities (Johnson, 1964; Wickman and Wiklund, 1983). Overshooting could help achieve both of these goals. Overshooting allows the pursuing dragonfly to come close to the invading dragonfly while avoiding collision. This rapid approach could invoke an evasive response from the invading dragonfly. This response would be evoked repeatedly in alternating directions as the pursuing animal overshoots from side to side (Fig. 2). An intriguing possibility is that the pursuer is in effect controlling the evasive responses of the evader to herd it out of the territory.

Finally, overshooting requires the pursuing animal to make repeated, high-magnitude turns (Fig. 2; Fig. 4). This behavior might function as a territorial display of flight performance. Displays of performance are common in male–male competitive interactions (Andersson, 1994; Enquist, 1985; Maynard Smith and Harper, 2003); they can cause a less competitive or less motivated animal to abandon the competition. Our results contrast with a previous study suggesting that dragonflies chasing conspecifics use a pursuit strategy that disguises the pursuing animal's approach against a constant background, i.e. motion camouflage (Mizutani et al., 2003). Here, we see no evidence of that strategy. The pursuer moves from one side of the evader to the other: a behavior that does not disguise its movement. We propose that the pursuer's visibility is part of a strategy that allows it to chase off invaders to its territory, and that sneaking up on the invader would not help it accomplish that goal.

In summary, we propose that by using an underdamped pursuit policy, territorial dragonflies achieve aggressive flight that showcases performance and drives away competitors while limiting the risk of collision and injury. As opposed to compensating for reaction delays, this behavior takes advantage of them, since delays are required to produce overshooting. Moreover, the relatively straight flight paths of efficient prey interception and the sinuous flight paths of male–male competitive pursuit can both be achieved using the same pursuit framework, but with modification of the pursuit parameters (gain, time delay and speed). This finding demonstrates the behavioral precision required for successful pursuit and emphasizes the functional changes that result from minor changes to an underlying behavior.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: A.C.L., A.J.C., T.L.H.; Methodology: A.C.L., A.J.C., T.L.H.; Software: A.C.L., A.J.C., T.L.H.; Validation: A.C.L., A.J.C., T.L.H.; Formal analysis: A.C.L., A.J.C., T.L.H.; Investigation: A.C.L.; Resources: T.L.H.; Data curation: A.C.L., T.L.H.; Writing - original draft: A.C.L., A.J.C.; Writing - review & editing: T.L.H.; Visualization: A.C.L., A.J.C.; Supervision: T.L.H.; Project administration: T.L.H.; Funding acquisition: A.C.L., T.L.H.

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Data availability

Raw and smoothed flight trajectory kinematics for the dragonfly chases examined here, along with all available metadata, can be found in Dryad (Lohman et al., 2019): [dryad.1hk66gf](https://doi.org/10.5061/dryad.1hk66gf)

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.190884.supplemental>

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